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The Relation of Certain Ecological Factors to the Inhibition of Forest Floor Herbs Under Hemlock

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Chromosome Numbers in Ten Species of Quercus, With Some Remarks on the Contributions of Cytology to Taxonomy

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THE RELATION OF CERTAIN ECOLOGICAL FACTORS TO THE INHIBITION OF FOREST FLOOR HERBS UNDER HEMLOCK

By REXFORD F. DAUBENMIRE

In the region of Turkey Run State Park, Parke county, Indiana, there occurs an abundance of Hemlock, *Tsuga canadensis*. In this locality the tree is to be found typically along the upper limits of precipitous creek bluffs and along the rims of the sandstone canyons,—here it is the dominant plant in an edaphic climax. The Hemlock association is a co-dominant climax with the typical Beech-Maple climax of the region.

One of the most notable features of this Tsuga association is the extreme absence of the usual forest floor herbs which are found in the Beech-Maple. Although these two associations occupy fairly comparable topographic positions, the upland Beech-Maple climax extending up to within a few meters of the canyon rims where it is replaced by the Tsuga, there is frequently a rather sharply drawn line between the two associations, so that within a few meters of each other there are two widely different types of forest floors, one (the Beech-Maple) rather rich in mesophytic herbs, the other exhibiting a carpet of leaves rarely interrupted by herbs. The common herbs of the Hemlock association are the saprophytes Monotropa and Epifagus, which at once seem to indicate the possibility of light as a controlling factor in the relative absence of herbs. Little observation is necessary to note, however, that there is a coat of well-dried needles and broad leaves under the Hemlock, while there is but a thin covering of damp, decomposing leaves under the Beech-Maple. This, together with the relative topographic positions of the two associations, suggested a possibility of evaporation as a limiting factor in herb development. Soil conditions, as evidenced by superficial examination alone, seem markedly contrasted in the two forest types. The soil under the Tsuga is of a loose texture, composed mainly of very fine sand of such a dry, non-plastic nature as to seem almost dust-like in comparison to the moist, plastic soil of the Beech-Maple.

A study has been made of four factors: evaporation, light, soil acidity and soil moisture, with an attempt to correlate differences in these respects between the Tsuga and Beech-Maple associations, with the differ-

ences in the forest floor herbs. The study includes the summer season, from June 17 to September 1, of 1929.

FLORISTIC DIFFERENCES

A statistical floristic difference between the two associations was obtained by the quadrat method. Twenty-five meter quadrats were plotted at fixed intervals from each other, in both associations, and maps were made showing the distribution and frequency of the plants. It was found that in twenty-five quadrats in the Beech-Maple there occurred: 14 species of herbs, 4 of shrubs and 7 of trees. In the Tsuga there were: 1 species of herb, none of shrubs and three of trees.

There is a wide difference in the relative numbers of herbaceous species as well as in the types of plants encountered. The only herb under the Tsuga was a saprophyte, Monotropa, which, judging from its frequency of appearance in the quadrats, was as dominant in the Hemlock as Sugar Maple was in the Beech-Maple. In October there was a vigorous growth of Epifagus under the Tsuga in as great abundance as was the Monotropa during the summer. All of the Beech-Maple herbs were chlorophyll-bearing.

Breaks in the Tsuga canopy are always oases populated by Dicranum, Polytrichum, Leucobryum, Cladonia, Mitchella, Polypodium vulgare, Chimaphila and Viburnum acerifolium. While these plants are typical for the more open spaces in the association, they are rarely if ever present in the more dense stand, save as occasional solitary individuals.

EVAPORATION AND LIGHT INTENSITY

Two atmometer stations were maintained during the summer, one in a typical spot in each association. A station consisted of four Livingston clay atmometer cups placed about one meter apart in a square, with the cups about two decimeters above the surface of the soil. Two cups were of the usual white type and two were treated with a black coating Livingston (4). Since the black atmometers differed from the white only in color, the difference in water loss between the two kinds, the black losing more through the greater absorbtion of light, was representative of the evaporative power of the light which penetrated the foliage canopy to the soil beneath. Evaporation from the two black and two white cups at each station was averaged and the results tabulated in Table I.

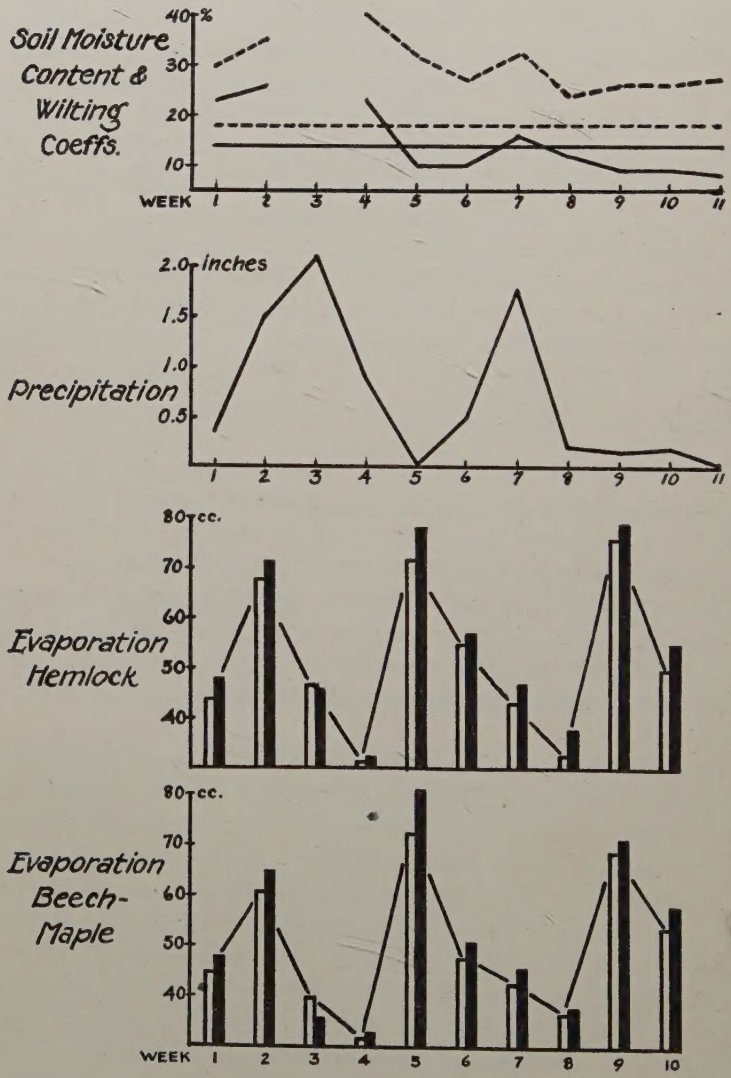
TABLE I. EVAPORATION IN CC WITH THE BLACK AND WHITE ATMOMETERS AVERAGED

WEEK ENDING	EVAPORATION IN CC IN BEECH MAPLE		EVAPORATION IN CC IN HEMLOCK	
	BLACK ATMOMETER	WHITE ATMOMETER	BLACK ATMOMETER	WHITE ATMOMETER
June 24	48.27	45.42	48.00	44.24
July 1	65.93	61.62	70.80	67.94
July 8	35.90	39.89	46.00	47.00
July 15	32.97	31.99	32.40	31.99
July 22	81.24	72.68	78.00	71.89
July 29	51.21	48.58	57.20	55.30
Aug. 5	49.06	43.64	47.20	44.24
Aug. 12	37.28	38.31	37.80	33.37
Aug. 19	71.63	67.94	79.60	76.63
Aug. 26	57.90	54.11	54.80	49.82
Average weekly evaporation	53.11	50.41	55.18	52.24
Average daily evaporation	7.58	7.20	7.89	7.46
Difference in average weekly evaporation: Black minus white	2.70		2.94	

This table shows that evaporation was practically the same in both associations, thereby indicating that it cannot be a critical factor in the inhibition of herb development under the Hemlocks. The situation having the greatest evaporation (as shown by the white atmometers alone) shifted constantly from one station to the other, and within narrow limits. The average daily evaporations were 7.20 cc and 7.46 cc in the Beech-Maple and Hemlock respectively. Figure 1 illustrates the coordination of seasonal fluctuations and types of atmometers in the two associations.

The results from the Beech-Maple evaporation agree with those results obtained by Fuller, Weaver, and Cain and Friesner, as summed up in the works of Cain and Friesner (2). The Hemlock evaporation, however, does not agree quite so well with the results of Moore *et al.* (5), who found that daily evaporation under Hemlock averaged 11.5 cc in four out of five of their stations. Their fifth station, one of a more northern location, and with an average daily evaporation of 7.5 cc, on the other hand, was quite similar to the results of Hemlock evaporation at Turkey Run. When the latter writers compared a different type of hardwood with the Hemlock, evaporation was found to be but little more of a critical factor than here, since the difference between the two types averaged .8 cc daily (.26 cc at Turkey Run).

FIGURE 1. SOIL MOISTURE CONTENT AND WILTING COEFFICIENTS, PRECIPITATION AND EVAPORATION, AVERAGED WEEKLY



Moore *et al.* (5) explain their increase in evaporation under Tsuga, at least partially, to the absence of herbaceous and shrub growth there. The situation at Turkey Run is evidently contrasted to the Eastern forests, since here most of the trees are comparatively young and the tenaceous lower branches, although for the greater part dead, persist to retard air currents. The majority of the Hemlock stands are in a fairly young state of development, probably due to previous suppression by giant white oaks, some of which still remain to break the uniformity of the stands. The age of the particular association in which these data were accumulated was unascertained. Selection of this stand, however, was based on average diameter of boles, which ranged from about 3-15 cm. d. b. h.

Figure 1 illustrates an interesting correlation between the depressions in evaporative power of the air and the periods of greatest precipitation. The rainfall peaks precede the evaporation depressions by one week in each case, demonstrating the direct relation of evaporation to relative humidity, which is in turn affected by rain.

Light radiation, as shown by differences between the black and white atmometers, was also practically the same in the two associations. Averaged over the entire summer, there was slightly less penetration in the Hemlock. Although this difference in penetration is quite constant, except for unexplainable reverses in the data in weeks three and eight, it is far too small to be of any significance as a critical factor of difference in herb development between the two associations.

The results of the black atmometers are not, in the opinion of the writer, successful as a measure of qualitative differences in light penetrating the two forest types. While there can be no doubt but that these cups measure light intensity quantitatively, with respect to its effect on evaporation, they certainly do not express the differences in kinds of light which may exist beneath the two forest types. A deficiency of one kind of light, for example, in the Hemlock, might be balanced in effect by a surplus of other kinds, so that the black atmometers show like light conditions as evidenced by evaporation, and still there may exist at the same time a difference in wave length of light exerting an inhibitive influence on the vegetation for physiological (photosynthetic) reasons. To the observer's eye, it seemed quite evident when the problem was forming itself that there was a considerable light difference under the trees of the two associations, but, from the results thus far obtained,

it must be stated that, quantitatively at least, solar radiation (as effecting evaporation on the two forest floors) is practically equal when determined by this method.

SOIL MOISTURE

For soil moisture studies, two series of soil samples were collected in each association weekly during the summer. A series consisted of a sample at each of the: 1″, 3″, 6″, 12″ and 18″ layers of soil. The soils were collected in air-tight tins and sent to the botanical laboratory at Butler University, where they were weighed, dessicated at 105 C for four or more days and reweighed to obtain the actual moisture content of the soils.

The moisture equivalents of the different soil depths tabulated herein are, with one exception, averages of four tests each on two soil samples of each soil layer selected at random from those used in the determination of moisture content. There was only slight variation in the four moisture equivalent tests of any one sample, and, since the variation between any two different samples of the same layer were also small, it was concluded that these averages are sufficiently accurate. Wilting coefficients of the soils were calculated from these moisture equivalents by the formula of Briggs and Shantz (1).

Soil moisture data are tabulated in Table II. By checking actual soil moisture with the wilting coefficients of Table III, it is found that in the Hemlock there is a negative amount of growth water from about the middle of July through the summer. The figures which are below the wilting coefficients for those depths, and therefore indicate a negative amount of growth water, are italicised. A two-inch rainfall on August 2 is reflected quite evidently in the upper half of the soil for this particular week. The line of effectual moisture penetration from this rain was between 6″ and 12″, but the moisture content was effected at least as low as 18″. Table IV and Figure 1 sum up the significant conclusions from the foregoing data. There is always an excess of soil moisture over the wilting coefficient, i. e., growth water, in the Beech-Maple, while in the Hemlock half or more of the summer weeks are characterized as extremely xerophytic edaphically, with the available water of most frequent occurrence in the uppermost layers. The absence of growth water in the soils of the Hemlock associations for such a great portion of the growing season is undoubtedly due to the fact that the

TABLE II. SOIL MOISTURE CONTENT AT DIFFERENT DEPTHS

Each figure represents a percentage of total water based on dry weight of the soil; each figure is an average of two different stations; italics signify the absence of growth water, i. e., an amount of water in the soil below the wilting coefficient.

	JUNE	JULY					AUGUST				SEPT.
Week Ending....	24	1	8	15	22	29	5	12	19	26	2
No. of wk.	1	2	3	4	5	6	7	8	9	10	11
Tsuga....1″	43.0	33.0	.....	42.5	*15.5*	*15.0*	22.8	27.4	*12.8*	*13.5*	*11.5*
3″	22.0	32.0	.....	22.5	*11.0*	*11.5*	18.0	*10.9*	*11.8*	*10.8*	*8.5*
6″	20.0	30.0	.....	21.5	*9.0*	*10.3*	18.3	*10.0*	*10.3*	*9.7*	*9.5*
12″	14.5	21.0	.....	17.5	*8.0*	*7.0*	*12.5*	*6.0*	*6.5*	*6.8*	*5.5*
18″	14.0	16.0	.....	12.5	*7.5*	*6.1*	*9.2*	*5.0*	*5.6*	*5.8*	*5.5*
Wkly. Av.	22.7	26.4	.....	23.3	*10.2*	*9.9*	16.2	*11.8*	*9.4*	*9.3*	*8.1*
Beech-Maple....1″	35.5	48.5	.....	69.5	40.9	33.0	37.0	28.9	34.7	37.5	33.5
3″	35.5	40.5	.....	39.0	38.5	31.8	36.0	26.3	28.2	32.0	32.0
6″	27.5	34.0	.....	34.0	29.2	24.7	29.9	22.2	24.7	24.0	26.0
12″	26.5	27.0	.....	30.6	24.3	21.1	29.8	21.2	21.8	21.5	20.5
18″	26.5	24.0	.....	26.8	25.6	22.7	25.5	20.2	21.5	15.5	24.0
Wkly. Av.	30.3	34.8	.....	39.9	31.7	26.6	31.6	23.7	26.1	26.1	27.2

TABLE III. AVERAGED SOIL MOISTURE CONTENT, WILTING COEFFICIENTS AND MOISTURE EQUIVALENTS FOR THE DIFFERENT SOIL DEPTHS

ASSOCIATION	DEPTH	AVERAGE S. M. C. 11 WEEKS	MOISTURE EQUIVALENT	WILTING COEFFICIENT
Hemlock	1″	23.7	29.45	16.0
	3″	15.9	30.61	16.6
	6″	14.5	29.32	15.8
	12″	10.5	23.20	12.6
	18″	8.7	20.01	10.8
Beech-Maple	1″	39.9	39.27	21.3
	3″	33.9	34.47	18.7
	6″	27.6	33.80	18.3
	12″	24.4	26.90	14.6
	18″	23.2	28.40	15.3

TABLE IV. SHOWING RELATIVE AMOUNTS OF AVAILABLE WATER DURING THE SUMMER IN THE TWO ASSOCIATIONS

		NO. OF WEEKS THERE WAS UNAVAILABLE WATER	PER CENT. OF SUMMER THERE WAS AVAILABLE WATER
Tsuga	1″	5	50
	3″	6	40
	6″	6	40
	12″	7	30
	18″	7	30
Beech-Maple	1″		
	3″		
	6″	0	100
	12″		
	18″		

roots of the Hemlock are massed in the upper few inches of soil, while in the case of the Beech-Maple no such massing of roots occurs. The fact that growth water was present, in the case of the Hemlock soils, in the upper layers more than in the lower layers, was undoubtedly due to the same reason (massing of roots), coupled with the distribution and extent of the rains which fell. That is, this layer of roots must have intercepted much of the rain which fell, otherwise the layer should, owing to greater water absorbtion, have been the drier and hence have had less growth water than the lower layers. It seems fairly certain that the soils under the Hemlocks were dry because of the presence of Hemlock, with its peculiar root formation, rather than the Hemlock being present where it is because the soil is dry. From these data, it seems that the amount of available moisture bears a direct relation to the richness of forest floor herbs.

Until recently the tremendous importance in some localities of soil moisture as a controlling factor in vegetational development has been underemphasized, especially in sylvicultural practice. The work of Fuller (3) in the dunes of Lake Michigan is an illustration of the relative unimportance of soil moisture, while Toumey (8) found soil moisture of paramount significance. The latter found that the roots of white pine depleted soil moisture progressively during the summer, which is quite in accord with the conditions under Hemlock at Turkey Run. A study of this factor by Thone (7) at Starved Rock, Illinois, brings out another similarity. This writer also found that there was no growth water in July and August, except immediately following periods of rain.

There is such a wide and obvious difference in the soil moisture relations of these two associations that this factor alone might be the decisive one in the development of floral carpets under the two forests.

SOIL ACIDITY

Samples of the soil were taken under typical stands of both associations at Turkey Run. Separated locations were selected under each forest type and at each location a series of ten samples were tested: five of the surface soil (just beneath the duff layer), and five corresponding subsoils (at about a six-inch depth). The soils were tested for their H-ion concentration by the quinhydrone method.

There were three such typical locations selected in the Beech-Maple and four in the Hemlock. The locations cover a four-mile line, extending from Turkey Run Creek to Mill Creek. Three pH readings were made of each sample, and the active acidities of each of the three readings were averaged to obtain an accurate active acidity average for the soil sample (Wherry 9). The results from 15 surface and 15 subsoils in the Beech-Maple, and 20 surface and 20 subsoils in the Hemlock are tabulated in Tables V and VI.

Figure 2 gives a graphic summation of the foregoing tables. The percentage of all samples taken in the particular layer in each association is shown at each pH interval. Thus 22.4 per cent. of the readings of surface soil samples taken under Hemlock had a pH value of 4.4. This table shows that there is a distinct difference in only the surface soil reaction. Although the occurrence of a difference in soil reaction between soils of contrasted vegetational types is not unusual, it frequently happens that when plotted on a scale the acid ranges overlap confusingly so as to render any conclusions only relative. Here, however, the acidity ranges of the two surface soils are separate and distinct, with an appreciable gap on the scale between the two. The difference in reaction of the surface soils alone might prove to be a limiting factor in a vegetational development, since it is the acid nature of this layer with which the seedlings of the association must first cope.

The subsoils prove to be more nearly alike. It is quite interesting and significant to note that the subsoils occupy an intermediate place on the scale, with the surface soils diverging each in an opposite direction, that of the Beech-Maple tending to be more neutral and that of the Hemlock more acid. These relative positions may be explained by

TABLE V. SOIL ACIDITY—BEECH-MAPLE

	SURFACE SOIL				SUBSOIL			
LOCATION	NO.	pH	ACTIVE ACIDITY	AV. ACTIVE ACIDITY	NO.	pH	ACTIVE ACIDITY	AV. ACTIVE ACIDITY
West of		6.1	8			4.6	250	
Falls	1	6.3	5	6	2	4.5	315	293
Canyon		6.3	5			4.5	315	
		6.7	1.5			5.0	100	
	3	6.6	2	2	4	5.1	80	101
		6.6	2			4.9	125	
		6.4	4			5.1	80	
	5	6.4	4	4	6	5.2	63	223
		6.5	3			5.1	80	
		5.3	50			4.9	125	
	7	5.4	40	43	8	5.0	100	117
		5.4	40			4.9	125	
		7.0	0			5.5	31.5	
	9	6.7	1.5	1	10	5.7	20	25
		6.6	2			5.6	25	
East of		6.6	12			5.1	80	
Boulder	1	6.8	1	1	2	5.2	63	68
Canyon		6.7	1.5			5.2	63	
		5.9	12.5			5.4	40	
	3	6.1	8	9	4	5.4	40	43
		6.1	8			5.3	50	
		6.9	0.5			5.3	50	
	5	6.8	1.0	0.7	6	5.5	31.5	40
		6.9	0.5			5.4	40	
		6.1	8			5.3	50	
	7	6.2	6	7	8	5.3	50	44
		6.2	6			5.5	31.5	
		6.1	8			5.1	80	
		6.1	8	7		5.1	80	80
		6.3	5			5.1	80	
Summer		6.0	10			5.8	16	
Evap.		6.1	8	9		5.7	20	17
Station		6.1	8			5.8	16	
		6.8	1			4.8	160	
		6.9	0.5	0.7		4.9	125	148
		6.9	0.5			4.8	160	

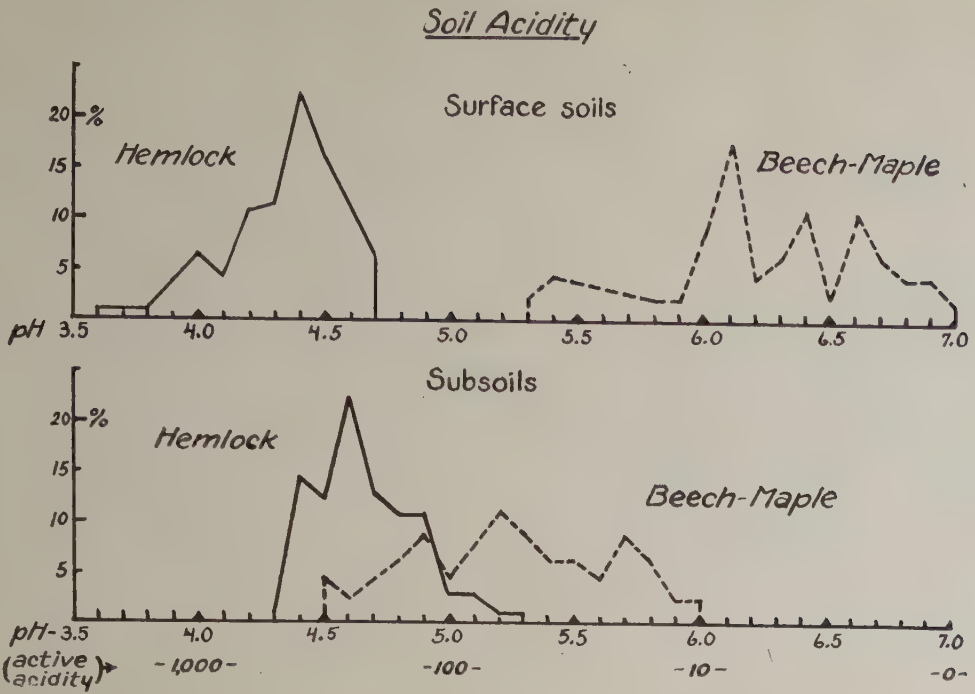
LOCATION	SURFACE SOIL NO.	pH	ACTIVE ACIDITY	AV. ACTIVE ACIDITY	SUBSOIL NO.	pH	ACTIVE ACIDITY	AV. ACTIVE ACIDITY
Summer		6.4	4			5.9	12.5	
Evap.		6.8	1	3		5.7	20	14
Station		6.4	4			6.0	10	
		6.0	10			5.6	25	
		6.4	4	5		5.7	20	20
		6.6	2			5.8	16	
		5.8	16			5.2	63	
		6.0	10	12		5.2	63	95
		6.0	10			4.8	160	

TABLE VI. SOIL ACIDITY—HEMLOCK

LOCATION	SURFACE SOIL NO.	pH	ACTIVE ACIDITY	AV. ACTIVE ACIDITY	SUBSOIL NO.	pH	ACTIVE ACIDITY	AV. ACTIVE ACIDITY
Summer		4.3	500			4.8	160	
Evap		4.6	250	417		4.9	125	116
Station		4.4	400			5.2	63	
		4.3	500			4.9	125	
		4.1	800	643		4.9	125	117
		4.2	630			5.0	100	
		4.4	400			4.4	400	
		4.4	400	400		4.4	400	400
		4.4	400			4.4	400	
		4.0	1,000			4.5	315	
	9	4.0	1,000	1,000		4.5	315	343
		4.0	1,000			4.4	400	
		3.6	2,500			4.4	400	
	7	3.8	1,600	2,033		4.4	400	400
		3.7	2,000			4.4	400	
East of		4.6	250			4.7	200	
Boulder	1	4.3	500	355	2	4.8	160	187
Canyon		4.5	315			4.7	200	
		4.2	630			5.1	80	
	3	4.2	630	553	4	5.3	50	70
		4.4	400			5.1	80	
		4.1	800			4.8	160	
	5	4.3	500	700	6	4.8	160	160
		4.1	800			4.8	160	

		SURFACE SOIL				SUBSOIL		
LOCATION	NO.	pH	ACTIVE ACIDITY	AV. ACTIVE ACIDITY	NO.	pH	ACTIVE ACIDITY	AV. ACTIVE ACIDITY
East of		4.3	500			4.9	125	
Boulder	7	4.2	630	710	8	4.9	125	117
Canyon		4.0	1,000			5.0	100	
		4.6	250			4.7	200	
		4.7	200	317		4.8	160	173
		4.7	200			4.8	160	
West of		4.4	400			4.5	315	
Falls	1	4.4	400	433	2	4.5	315	315
Canyon		4.3	500			4.5	315	
		4.6	250			4.6	250	
	3	4.5	315	293	4	4.6	250	250
		4.5	315			4.6	250	
		4.6	250			4.3	500	
	5	4.5	315	322	6	4.4	400	433
		4.4	400			4.4	400	
		4.5	315			4.6	250	
	7	4.4	400	343	8	4.6	250	233
		4.5	315			4.7	200	
		4.5	315			4.9	125	
	9	4.2	630	525	10	4.9	125	167
		4.2	630			4.6	250	
Mill		4.2	630			4.6	250	
Creek	1	4.3	500	543	2	4.5	315	272
		4.3	500			4.6	250	
		4.4	400			4.7	200	
	3	4.4	400	400	4	4.6	250	217
		4.4	400			4.7	200	
		4.4	400			4.6	250	
	5	4.6	250	350	6	4.6	250	250
		4.4	400			4.6	250	
		4.6	250			4.5	315	
	7	4.7	200	650	8	4.5	315	293
		4.7	200			4.6	250	
		4.5	315			4.7	200	
	9	4.5	315	315	10	4.7	200	217
		4.5	315			4.6	250	

FIGURE 2. SUMMATION OF FOREGOING TABLES



the nature of the substratum. Mansfield sandstone, which is quite soft and easily decomposing, underlies most of the soil at Turkey Run. The soil is quite thin and is presumably affected by the silicious substratum which on decomposing produces acid conditions. The divergent types of leaves which are shed on the two types of forest floors evidently tend to alter the reaction of the upper soil layers in a similar divergent manner. Although the proximity to a precipitous bluff or canyon rim is at Turkey Run inevitable with a Hemlock stand, it is evident from the nature of the water relations of the Hemlock soil, as shown above, that the leaching out of bases is not entirely responsible for such a difference in acidity. The soil is always quite dry, and the soil moisture data show that precipitation only slightly affects the moisture content of the soil and that very little water gets beyond the reach of the roots.

It is of common occurrence that, as any condition of environment extends itself in either direction from the optimum, the numbers of species decrease. The conditions of soil reaction and statistics of vegetational frequency in the two associations at Turkey Run coincide remarkably with Olsen's (6) concept, but whether or not acidity is the principal factor inhibiting herbs under the Hemlock cannot be empirically stated; however, the increase in acidity between the two associations and the decrease in species are at least concomitant phenomena.

That acidity does play a part in the vegetational development under the Tsuga may be demonstrated by a review of the plants which first inhabit this forest floor under a break in the foliage canopy. Since Monotropa, Epifagus and Viburnum acerifolium grow in both associations, it may be concluded that they are tolerant of quite a range of acidity,—from 3.7 to 7.0. Cladonia, Leucobryum, Dicranum, Polytrichum and the ericads, Gaylussacia and Chimaphila, are notoriously plants of acid soils, and it is naturally expected that they are to be found in relative abundance only under the more acid conditions of the Tsuga. The presence of these plants rehabitating Tsuga soil is indicative of the high acidity acting at least as a contributing factor in vegetational development.

SUMMARY

1. The purpose of these investigations was to correlate, if possible, differences between Hemlock and Beech-Maple forest types in four factors of the habitat (evaporation, light intensity, soil moisture and

soil acidity) with the differences in forest floor herbs,—the Hemlock being quite barren of herbs, while the Beech-Maple, in a comparable topographic situation, has a rich carpet of forest floor herbs. This study included the summer weeks, from June 17 to September 1, of 1929.

2. Evaporation results indicate an equal degree of mesophytism in the two associations, in contrast to the work of Moore *et al.*, who found Hemlock forests to be slightly more xerophytic in respect to evaporation than hardwood.

3. Light intensity, as measured by difference in evaporation between black and white atmometers, was practically equal, quantitatively at least, in its effect upon water loss in the two associations.

4. Soil moisture studies showed a lack of growth water in the Hemlock soil from about the middle of July through the summer, except for a short period immediately following a heavy rain. The lower layers of soil under Hemlock are more constantly lacking in growth water, due to the slight penetration of rainfall. Growth water was always present in all soil layers studied in the Beech-Maple.

5. Soil reaction varies widely between the two forest types in only the surface soils. The surface soil in the Hemlock ranges from superacid (pH 3.6) to mediacid (4.7), and this layer in the Beech-Maple ranges from subacid (5.3) to circumneutral (7.0).

6. It is concluded, therefore, that, of the factors studied, soil moisture conditions exerted the most inhibitive influence on vegetational development under Hemlock, while the greater acidity of the surface soil in the Hemlock is probably a contributing factor in the inhibition of forest floor herbs.

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Chromosome Numbers in Ten Species of Quercus, With Some Remarks on the Contributions of Cytology to Taxonomy

By Ray C. Friesner

INTRODUCTION

It is becoming increasingly more apparent that for the solution of many of the difficult problems in the field of taxonomy, we must take into consideration the work of the cytologist. A very large number of what we may call cytological-taxonomic studies have appeared during the past decade. These have thrown much light upon such taxonomic problems as the origin, evolution, and relationship of species within polymorphic genera; the determination of the limits of subgenera and of variable species with numerous supposed variations, and the probable relationship of supposed natural hybrids.

CYTOLOGICAL CHARACTER OF POLYMORPHIC GENERA

When we turn to the cytological character of genera containing large numbers of species, particularly those which contain many taxonomic entities which are puzzling to know whether they should be considered species, or varieties, or hybrids, and if the latter two, the problem of determining just which particular species should claim a particular form as its variety, or just which species were the probable parents of a hybrid, we find that these genera fall into four cytological categories. There are (1) polyploid genera, (2) genera with both polyploid and aneuploid species, (3) genera with species containing chromosome numbers so variable that it is difficult to place them in either group (1) or (2), and (4) genera in which all species appear to have the same chromosome numbers.

Polyploid genera. Table I gives a list of ninety-six genera in which species occur with chromosome numbers forming a geometrical series with some small number as the basic number. This table is a complete list of such genera studied to date where the publication is known to the writer. There are undoubtedly others. In the third column, figures refer

TABLE I

Genera with polyploid species

GENUS	BASIC CHROMOSOME NUMBERS	POLYPLOID GROUPS (Number of Chromosomes in sporophyte tissue)	AUTHORITY[1]
Typha	15	2x, 4x	165
Elodea	8	2x, 6x	65, 174
Vallisneria	10	2x, 4x	85, 217
Triticum	7	2x, 4x, 5x, 6x, x(haploid)	1, 43, 92, 94, 95, 96, 126, 145, 146, 160, 173, 203, 206, 210, 211, 212
Avena	7, (8?)	2x, 4x, 6x	32, 33, 45, 46
Hordeum	7	2x, 4x, 6x	1, 56
Zea	10 (7, 8, 9, 11, 12)	2x, 3x, 4x	42, 117, 125, 161
Aegilops	7	2x, 4x, 5x, 6x	1, 46, 160, 179
Sorghum	5	2x, 4x, 8x	120
Euchlena	10	2x, 4x	1, 112
Scirpus	8?	2x, 4x?	60, 215
Anthurium	15 (25?)	2x, 4x	48
Tradescantia	6	2x, 3x, 4x	189, 202
Haworthia	7	2x, 4x	41, 202
Hyacinthus	8	2x, 3x, 4x	33, 132
Allium	(7) 8	2x, 4x	23, 70, 106
Musa	8, (11)	2x, 4x, 6x	34, 204
Muscari	9, 11	2x, 4x	36, 133
Narcissus	8	2x, 3x, 4x	131, 191
Tulipa	8, 12	2x, 3x, 4x, 5x	131, 140, 207
Spiranthes (Gyrostachys)	15	2x, 4x	158
Platanthera	21	2x, 6x	3
Dendrobium	20	2x, 4x	72
Oncidium	14	2x, 4x	72
Vanda	8	2x, 4x	72
Salix	19	2x, 3x, 4x, 6x	
	22	4x	12, 59
Populus	19	2x, 4x	12
Betula	14	2x, 3x, 4x, 5x, 6x	66, 218
Alnus	14	2x, 4x	213, 219
Morus	14	2x, 3x	153

[1]Numbers in parentheses refer to titles in bibliography. No attempt has been made to give a complete list of titles. Latest titles which will serve as leads to students working on particular genera are all that are given.

GENUS	BASIC CHROMOSOME NUMBERS	POLYPLOID GROUPS (Number of Chromosomes in sporophyte tissue)	AUTHORITY
Rumex	7, 8, 10	2x, 4x, 6x, 8x, 10x, 12x, 20x	81, 82, 97, 98, 151, 160
Polygonum	(10) 11	2x, 4x	81
Rheum	11	2x, 4x	81
Silene	12	2x, 8x	10
Dianthus	15	2x, 4x, 6x	163
Ranunculus	7	2x, 4x	182, 190, 215
Thalictrum	12	2x, 4x	
	7	2x, 4x, 6x, 8x, 10x, 12x	99, 101, 155
Alyssum	8	2x, 4x	83, 100
Arabis	8	2x, 4x	83
Brassica	8, 9, 10	2x, 4x	49, 89, 91, 143, 185
Draba	8	2x, 4x, 6x, 8x, 10x	63, 64
Bursa (Capsella)	8	2x, 4x	69
Erysimum	8	2x, 4x, 6x, 8x	83
Drosera	10	2x, 3x, 4x	166
Saxifraga	15	2x, 4x	157
Vicia	6, 7	2x, 4x	195
Trifolium	7, 8	2x, 4x, 6x, 10x, 16x+2	17, 18, 90, 214
Rosa	7	2x, 3x, 4x, 5x, 6x, 8x	9, 11, 13, 39, 76, 159, 196
Rubus	7	2x, 3x, 4x, 5x, 6x, 8x	109, 110, 113, 115
Crategus	16	2x, 3x, 4x	109, 111
Fragaria	7	2x, 6x, 8x	78, 115, 116, 122, 220
Prunus	8	2x, 3x, 4x	147, 148
Pyrus (Inc. Malus)	(14) 17	2x, 4x	172, 186
Alchemilla	16	2x, 4x	194
Potentilla	8	2x, 4x	44
Linum	8, 9, 10	2x, 3x, 4x, 6x	38, 124, 208
Oxalis	7 (5, 10, 11, 12)	2x, 4x, 6x	65
Pelargonium	(8) 9	2x, 4x, 5x, 9x, 10x	200
Citrus	9	2x, 4x	114
Acer	13	2x, 4x, 6x	32, 201
Aesculus	20	2x, 4x	71, 189
Fugosia	10	2x, 6x	119
Gossypium	13	2x, 4x	6, 37
Hypericum	8, 9, 10	2x, 4x	22, 144
Viola	6, 10, 12 (7, 8, 11, 13, 17)	2x, 3x, 4x, 5x, 6x, 7x, 8x, 9x	24, 25, 51, 129
Oenothera	7	x, 2x, 3x, 4x	19, 28, 50, 121, 178, 184

GENUS	BASIC CHROMOSOME NUMBERS	POLYPLOID GROUPS (Number of Chromosomes in sporophyte tissue)	AUTHORITY
Fuchsia	11 (14)	2x, 3x, 4x	209
Godetia	7 (9)	2x, 6x	57
Aucuba	8	4x	127, 213
Vaccinium	12	2x, 4x, 5x, 6x	118
Primula	9	2x, 4x	
	11	2x, 4x	79, 142, 205
	12	2x, 3x	
Verbena	4	2x, 3x	88
Mentha	9	2x, 4x	180
Galeopsis	8	2x, 4x	134
Datura	12	x, 2x, 3x, 4x (2x+1, 2x+1+1, 2x+2, 4x+1, 4x+2, 4x−1)	8, 14, 16, 149
Petunia	7	2x, 4x	183, 207
Physalis	12	2x, 4x	207
Nicotiana	8, 9, 10, 12	x, 2x, 3x, 4x	27, 52, 53, 54, 55, 171, 207
Lycopersicum	12	x, 2x, 3x, 4x	103, 104, 105, 108
Solanum	12	2x, 4x, 6x	45, 86, 107, 193, 207
Digitalis	28	2x, 4x	21
Veronica	8	2x, 3x, 4x, 6x, 8x	
	7	2x, 4x	75, 208
	9, 10, 17	2x	
Plantago	6 (4, 5, 10)	2x, 4x	65, 187
Lonicera	9	2x, 4x	208
Valeriana	7	2x, 4x, 8x	183
Campanula	8, 17 (10, 13)	2x, 4x, 6x	47, 63, 208
Lobelia	7 (9?)	2x, 4x, 6x	208
Crepis	3, 4, 5, (6?)	x, 2x, 3x, 4x, 5x, 6x, 8x	4, 5, 73, 123, 135, 136, 137, 138, 139, 168
Aster	9	2x, 4x, 6x	198
Senecio	5?	2x, 4x, 8x, 10x, 12x, 18x	2
Lactuca	(5, 7, 9)		
	8	2x, 3x, 4x, 6x	63, 80
Hieracium	7, 9, 17	2x, 4x, 6x	154, 167
Chrysanthemum	9	2x, 3x, 4x, 5x, 6x, 8x, 10x	197, 199
Erigeron	9		
	(8, 13)	2x, 3x, 4x, 6x	74
Taraxacum	8 (13)	2x, 4x	181, 192
Dahlia	16 (18)	2x, 4x	102

to the number by which the basic number must be multiplied to give the number of chromosomes occurring in sporophyte tissues of different species within the genus. It will be seen that multiples run more often 4, 6, and 8, but occasionally run as high as 16, 18, or 20. Numbers in the fourth column refer to literature citations. No attempt has been made to give a complete bibliography. This would be both too costly of time and space as well as entirely unnecessary, since citations given are "key" references.

Aneuploid (dysploid) species. Table II lists six genera in which species have chromosome numbers which are slightly more or slightly less than exact multiples of the basic number. In the table, 2x+1 indicates that some one particular pair is represented by three chromosomes forming what has been called a "trisome," 2x+1+1 indicates that one each of two different pairs is so represented, thus forming two "trisomes," while 2x+2 indicates that some one particular pair is represented by four chromosomes, thus forming a "tetrasome." The relatively small number of genera listed in this table may or may not be significant. If it is significant, it would indicate that there is a much greater tendency for all members of a chromosome set or complement to double than for individual chromosomes so to behave.

TABLE II

Genera with species showing aneuploidy

GENERA	BASIC CHROMOSOME NUMBERS	ANEUPLOID GROUPS (Number of chromosomes in sporophyte tissue)	AUTHORITY
Hyacinthus	8	3n−1, 2n+3, 3n+2, 3n+4	33
Betula	14	6x+6, 3(2x+2)*	218
Rosa	7	2x+1, 2x+2	39
Enothera	7	2x+1, 3x+1, 4x+2	50
Lycopersicum	12	2n+1	105
Datura	12	2x+1, 2x+1+1, 2x+2, 4x+1, 4x+2, 4x−1	14, 15

Genera with chromosome numbers irregular. Table III lists twelve genera in which the chromosome number is so irregular that further

*This arrangement is suggested by the present writer as possible. It was not proposed by Woodworth (26).

study will be necessary in order to determine which are basic numbers and to determine the condition with respect to polyploidy or aneuploidy. some of these genera (e. g., Campanula, Lactuca, Viola, Oxalis, and Plantago) belong also to the polyploid group, and it is entirely possible that further study will reveal two or more basic numbers, as is true in the genus Crepis (and possibly others), and the apparent irregular numbers will be found to fall in line with polyploidy and aneuploidy which is so common.

TABLE III

Genera with chromosome numbers so irregular that further study is necessary to determine which are basic numbers and to determine the condition with respect to polyploidy and aneuploidy

GENERA	HAPLOID CHROMOSOME NUMBER RANGE	AUTHORITY
Cyperus	17, 21, 48, 54, 73	221
Eleocharis	5, 8, 9, 15, 18, 19, 26-29	221
Scirpus	8, 10, 13, 18, 19, 20, 21, 22, 23, 25, 28, 30, 31, 33, 34, 38, 39, 50, 52, 53, 54, 55, 64	58, 60, 67
Carex	9, 15, 16, 19, 23, 24, 26, 27, 28, 29, 31, 32, 33, 34, 35, 36, 37, 38, 40, 41, 42, 56	61, 62, 63, 87
Tradescantia	6, 7, 8, 9, 10, 11, 12, 13, 14	189
Linum	8, 9, 10, 14, 15, 16, 30	38, 124, 208
Oxalis	(7, 14, 21) 5, 10, 11, 12, 40	65
Callitriche	3, 5, 10, 19	84
Viola	6, 7, 10, 11, 12, 13, 17, 18, 20, 24, 26, 27, 30, 36, (6, 12, 18, 24, 30, 36)	24, 129
Begonia	10, 14, 20	65
Plantago	(6, 12) 4, 5, 10	65
Campanula	10, 13, (17, 34, 51), (8, 16, 32)	63, 208
Senecio	5, 10, 18, 19, 20, 23, 24, 25, 26, 30, 90	2
Lactuca	5, 7, 9, (8, 12, 16, 24)	63, 80
Erophila	7, 15, 32	216

Genera with but one chromosome number. Table IV lists ten genera in which five or more species have been studied and but a single chromosome number found applicable to all species. In only two cases, viz., Philadelphus and Corylus, has the number of species studied been large. It may, therefore, well be that these genera will, after further study, also be transfered to groups I and II. The relatively small number of genera in this group at least serves to indicate how relatively frequent is the condition, polyploidy. Further study upon these genera

will be necessary before constancy of chromosome number, with whatever it may imply from a phylogenetic standpoint, may be a definitely proven condition in these genera.

TABLE IV

Genera in which five or more species or varieties (all studied to date) show the same chromosome numbers

GENERA	NO. OF SPECIES	HAPLOID CHROMOSOME NUMBER	AUTHORITY
Pinus	7	12	40
Lilium	6	12	30, 130, 175, 176, 177
Cypripedium	5	11	156
Corylus	17	14	219
Quercus	10	6	Present Paper
Ficus	7	13	29, 217
Philadelphus	37	13	7
Wisteria	7	8	164
Scabiosa	8	8	162
Pentstemon	8	8	65

CYTOLOGICAL DATA BEARING ON THE LIMITS OF SUBGENERA

Clausen (25) has shown how well cytology may help in the determination of the limits of subgenera groups. He has shown, for example, that the Nominium section of Viola should be divided into two subsections, one with species having chromosomes in multiples of 10 and the other with species having chromosomes in multiples of 12, that the Chamaemelanium section includes only forms with numbers of x=6 and x=12, while section Melanium contains species with such variable counts as x=7, 8, 10, 11, 13, 17, 18, 20, 24, 30.

In the wheats it is found that members of different sections of the genus have different chromosome numbers, viz., Monococcum wheats have 7 as the haploid number, Emmer wheats have 14 and Spelt wheats have 21 as the reduced number. In the roses (63): Section Caninae species have $7\times2=14$, $7\times2+14=28$, $7\times2+21=35$, and $14\times2+28=56$; in section Cinnamomea species have 7, 14, 21, and 28 pairs. In Lactuca (63) subgenus Lactuca has 9 pairs, subgenus Crepidastrum has 5 pairs, and subgenus Ixeris has 7, 8, 12, 16, and 24 pairs. Afzelius (2)

has shown in the genus Senecio that species in the section Obejacoideae have 10 pairs of chromosomes, in section Obejaceae and in a number of others the haploid number is 20, while in section Tephroseris it is 25. Numerous other examples occur in the literature.

CYTOLOGICAL DATA BEARING ON SPECIES LIMITS

All attempts to define and therefore definitely delimit the term species break down sooner or later in their application. The term will undoubtedly best serve its purpose by continuing to denote "an aggregate of more or less similar individuals which may be considered a kind." I would not advocate any basis of delimitation which did not embody the element of "convenience" in observational determination. Nevertheless, cytological data has something to offer—only substantiating evidence, it is true—toward determining species limits when a particular species has a wide range of variability and what may seem to be more or less distinct entities within the supposed single species. An example is found in the case of *Betula alba L. (B. pubescens* Ehr.). *B. verrucosa* Ehr. and *B. papyrifera Marsh.* are often considered to be but extreme forms of *B. alba* L. It has been shown by Helms and Jorgensen (66) that *B. verrucosa* has 14 and *B. alba* has 28 as the haploid chromosome numbers, while Woodworth (218) has found *B. papyrifera* to be pentaploid, with 35 as the reduced number. From this it would seem that *B. verrucosa* and *B. papyrifera* should each be considered as species coordinate with, and not forms of, *B. alba.*

A slightly different aspect of this same type of contribution of cytology to taxonomy is found in the aid it may give in helping determine the status of a supposed taxonomic variety. An example is found in the case of *Betula papyrifera* var. *cordifolia* (Regal) Fernald. It has been shown by Woodworth (218) that *B. papyrifera* is pentaploid (x=35) while *B. papyrifera* var. *cordifolia* is tetraploid (x=28). From this it would seem that *B. cordifolia* should be recognized as a species distinct from *B. papyrifera.*

Blackburn (10) found two races of *Silene ciliata* to yield 12 and 48 respectively as haploid numbers, and, in case these chromosome differences are correlated with constant visible morphological differences, it would seem justifiable to separate the species into two species.

CYTOLOGICAL DATA IN RELATION TO NATURAL HYBRIDS

The cytological behavior of known hybrids has been studied by many workers. In some cases hybrids behave perfectly normally cytologically; in others the chromosome number of the hybrid is twice as many as the sum of the two gametes instead of being equal to the sum of the two; and in many, while chromosome numbers equal the sum of the two gametes, the cytological behavior of the hybrid is very abnormal. Doubling of the number of chromosomes by hybrids is found in such genera as Papaver (170), Rosa (13), Nicotiana (26) and others. Among the cytological behaviors which are commonly looked upon as evidence of past hybridity, the following may be cited: abnormal meiosis, chromosome lagging in meiotic anaphase, imperfect pairing in meiosis, chromosome extrusion and formation of dwarfed and degenerate microspores, cytomyxis, pollen sterility, and polyploidy.

Cytology may offer evidence bearing upon possible relationships of supposed natural hybrids. Example is found in the case of *Betula coerulea* Blanchard, as pointed out by Woodworth (218). This form is variously considered a natural hybrid between *B. coerulea grandis* and *B. populifolia* and between *B. papyrifera* and *B. populifolia*. Cytological data, according to Woodworth, makes the latter relationship improbable, since *B. coerulea* is diploid (x=14), while *B. papyrifera* is pentaploid (x=35) and *B. populifolia* is diploid (x=14). The former relationship is cytologically possible, since *B. coerulea grandis* is also diploid. Numerous other illustrations might be given.

CHROMOSOMES IN THE GENUS QUERCUS

Chromosome studies in the Fagales have been made upon Betula (66) (218), Corylus, and Alnus (213) (219). In Betula a polyploid series (2x, 3x, 4x, 5x, 6x), with 14 as the basic haploid number, is found. In Corylus three species according to Wetzel (213), show 11 as the haploid number, while in Alnus five species show 14 as the haploid number. In a paper which appeared just as this paper was ready for the press, Woodworth (219) finds 14 as the haploid number in 17 species of Corylus and 14 as the basic number of a 2x and 4x series in Alnus. No member of the Fagaceae has been studied to date.

Acorns from the following species of oaks were collected in the

autumn of 1928: *Quercus alba* L., *Q. macrocarpa* Michx., *Q. Prinus** L., *Q. Michauxii* Nutt., *Q. muhlenbergii* Engel., *Q. borealis maxima* Ashe. (*Q. rubra* of Gray's Manual), *Q. velutina** Lam., *Q. coccinea* Muench., *Q. marilandica** Muench., and *Q. prinoides* Willd*.

These acorns were planted in moist sawdust in the greenhouse at varying dates during the autumn and early winter. Acorns of *Q. Prinus* had already germinated in the field before they were collected. The radicle and most of the hypocotyl were severed from each and they were then planted in the moist sawdust with approximately 2 centimeters of the hypocotyl protruding from the acorn. In all cases these hypocotyls regenerated 2-5 vigorous new radicles. When the radicles from any particular acorns reached 4-5 centimeters they were removed and washed free from sawdust particles and the root tips were killed in strong chromo-osmic-acetic solution according to Flemming's formula. Germination and regeneration data collected during this work will be presented in a subsequent brief paper, since it has no direct bearing upon the question at hand in this paper.

Root tips were washed free from the killing solution, dehydrated, and brought into paraffin. They were sectioned 12 microns thick and stained in iron haematoxylin. All chromosome counts were made with a Spencer research microscope equipped with apochromatic objectives and aplanatic condenser, and at a magnification of 1900 X. Counts were made from both side and polar views of both the metaphase and early anaphase stages of somatic mitosis.

OBSERVATIONS

Q. alba (2x=12). Figures 1, 2, 15, 16. Chromosome behavior is apparently normal. Figure 2 shows one chromosome in metaphase plate split before the remaining members have begun to divide. Figure 1 shows four daughter chromosomes (1 pair) considerably larger than the others. This was not a constant features of this species.

Q. macrocarpa (2x=12). Figures 3 and 4. Chromosome behavior normal in every way. Chromosome count of 12 as the diploid number is certain. Figure 3 must have been drawn from a cell in early metaphase. Nuclear membrane had already disappeared but the nu-

* Acorns from *Q. Prinus*, *Q. velutina*, and *Q. marilandica* were collected by Mr. Ralph Wilcox, Indiana State Forester, and those of *Q. prinoides* were supplied by Mr. Charles Deam from his Arboretum at Bluffton, Indiana.

cleolus marked "n" had only begun to disorganize. The conclusion that it was disorganizing is based upon the ragged contour which it exhibited.

Q. Prinus (2x=12). Figures 17 and 18. Chromosome behavior apparently normal. One chromosome in figure 17 marked "a" has begun division earlier than others. No other abnormalities were observed in this species.

Q. Michauxii (2x=12). Figures 19-21. Chromosome behavior slightly abnormal. A single case of non-disjunction affecting two chromosomes is shown in figure 21. This resulted in 14 chromosomes moving toward one pole and but 10 toward the other. Occasional cases of tardy departure from metaphase plate were also found.

Q. muhlenbergii (2x=12). Figures 5, 22, and 23. Chromosome behavior somewhat abnormal. Figures 5 and 22 show normal behavior with 12 daughter chromosomes for each pole of the dividing cell. Figure 23 shows only 16 chromosomes. Eight are widely separated while 8 others are in close proximity to each other. It is possible that 8 of these represent daughter chromosomes and the other 8 represent chromosomes tardy in their longitudinal division. In that case the normal number of 24 daughters would ultimately be produced. A number of cases of tardy separation of daughter halves were found and this is a bit of evidence in favor of the probability that 8 of the chromosomes in figure 23 are undivided and 8 divided.

Q. borealis maxima (2x=12). Figures 6, 7, and 24. Chromosome behavior slightly abnormal. Figures 6 and 7 show normal behavior in polar views of metaphase and early anaphase respectively. Figure 24 shows a slight tardiness in the separation of three sets of daughter chromosomes.

Q. velutina (2x=12). Figures 8 and 25. Chromosome behavior normal. Figure 8 shows 24 daughter chromosomes in polar view of early anaphase and figure 25 shows 12 daughters moving toward each pole.

Q. coccinea (2x=12). Figures 9-11. Chromosome behavior somewhat abnormal. Figure 9 shows polar view of an early anaphase with 25 daughter chromosomes. This must have been due to an extra longitudinal split on the part of one chromosome or it could have resulted from failure to divide on the part of a thirteenth chromosome which could have been present before nuclear division as a result of previous non-disjunction. Figures 10 and 11 show normal behavior in

polar views in anaphase and metaphase. Figure 11 shows the disorganizing nucleolus marked "n."

Q. marilandica (2x=12). Chromosome behavior normal. Figure 12 shows polar view of early anaphase with 24 daughter chromosomes.

Q. prinoides (2x=12). Figures 13, 14, and 26. Chromosome behavior normal. Figure 13 shows 12 daughter chromosomes in polar view of late anaphase. Figure 14 shows 24 daughters in polar view of very early anaphase. Figure 26 shows side view of very early anaphase, with 12 longitudinally split chromosomes.

DISCUSSION

A haploid number so low as 6 is interesting when the other three genera studied in the order Fagales show 11 and 14 as their reduced numbers. If polyploidy is absent in the genus Quercus, this will also be a significant fact. Too few species, however, have been studied to warrant any such conclusion at present.

Just as the manuscript for this paper was going to print a paper appeared by Woodworth (219) in which he found that the basic number 14 also holds for Alnus, and that tetraploid species have 28 as the reduced number. Wetzel (213) had previously reported 14 as the reduced number, but found only diploids. Wetzel had reported 11 as the reduced number for Corylus, but Woodworth finds the number to be 14 in his studies. Seventeen species, varieties, and hybrids indicated no evidence of polyploidy. This is of considerable interest, in view of the lack of evidence for polyploidy in Quercus. An attempt will be made to secure material for study of many other species as well as of some of the numerous hybrids which have been described.

It has been pointed out by Osawa (152), Longley (116) and others in Taraxacum, Fragaria, Rosa, Rubus, et al., that within any closely related group, species with smaller chromosome numbers are more primitive and those with larger numbers are more recent in their phylogeny. If this is true, the genus Quercus is more primitive than Betula, Corylus and Alnus. It has, however, been claimed with equal reason in the case of Maize and its relatives (Longley, 112) that more primitive and less specialized members have higher chromosome numbers and more recent and more highly specialized members have lower chromosome numbers. Heilborn (63) expresses the opinion that in case one

group of species is considered for other reasons to be derived from another, the group with the lower chromosome number should be regarded as the more primitive and that with the higher number as the more recent. While phylogenetic lines may be drawn from groups with low to groups with higher chromosome numbers, chromosome numbers alone are insufficient for constructing a phylogenetic structure and are only valuable as supplementary evidence.

From the standpoint of mitotic behavior it would seem that abnormalities and irregularities are too infrequent to indicate anything against considering all of the forms studied in this paper to be bona fide species. It is true that most of the mitotic criteria used for such conclusions are determined only in meiotic divisions, and hence conclusions of this nature based upon mitotic behavior above described are of little value. It should also be noted that chromosome counts based upon cells of roots may be misleading, since it has been shown by Breslawetz (20) and Langlet (101) that individual root cells may have as high as 4x and 8x chromosome numbers and entire roots may exhibit 4x numbers. This could hardly be misleading in the case of Quercus, however, since the number in root cells is already low. No cells were found in this study illustrating the above situation as Langlet found it in *Spinacea oleracea, Thalictrum spp.,* and *Cannabis sativa.*

SUMMARY

1. Chromosome studies reveal 12 as the diploid number of chromosomes in the roots of each of ten species of oaks.

2. Mitotic behavior is regular and normal in six of the ten species.

3. Four species show such mitotic abnormalities as somatic nondisjunction, tardy separation of daughter halves, and extra longitudinal division of a single chromosome.

4. Tables are included listing 96 genera with references in which polyploidy and aneuploidy has been found.

5. Other tables list genera exhibiting variable chromosome numbers and genera having all species with the same numbers.

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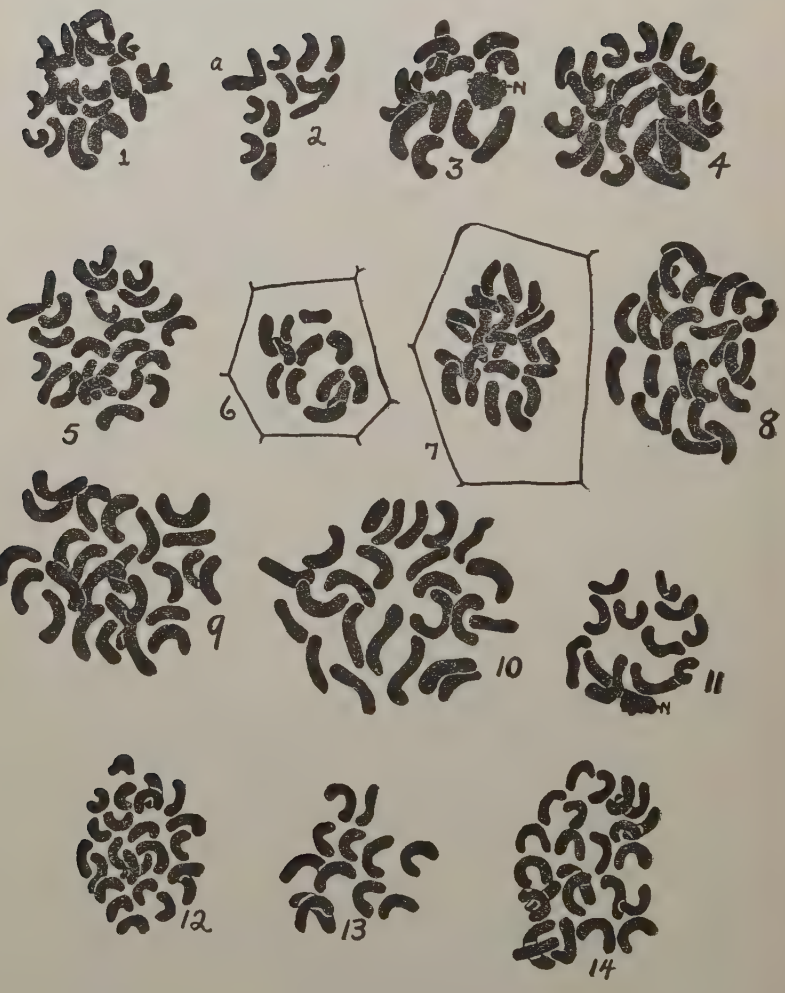
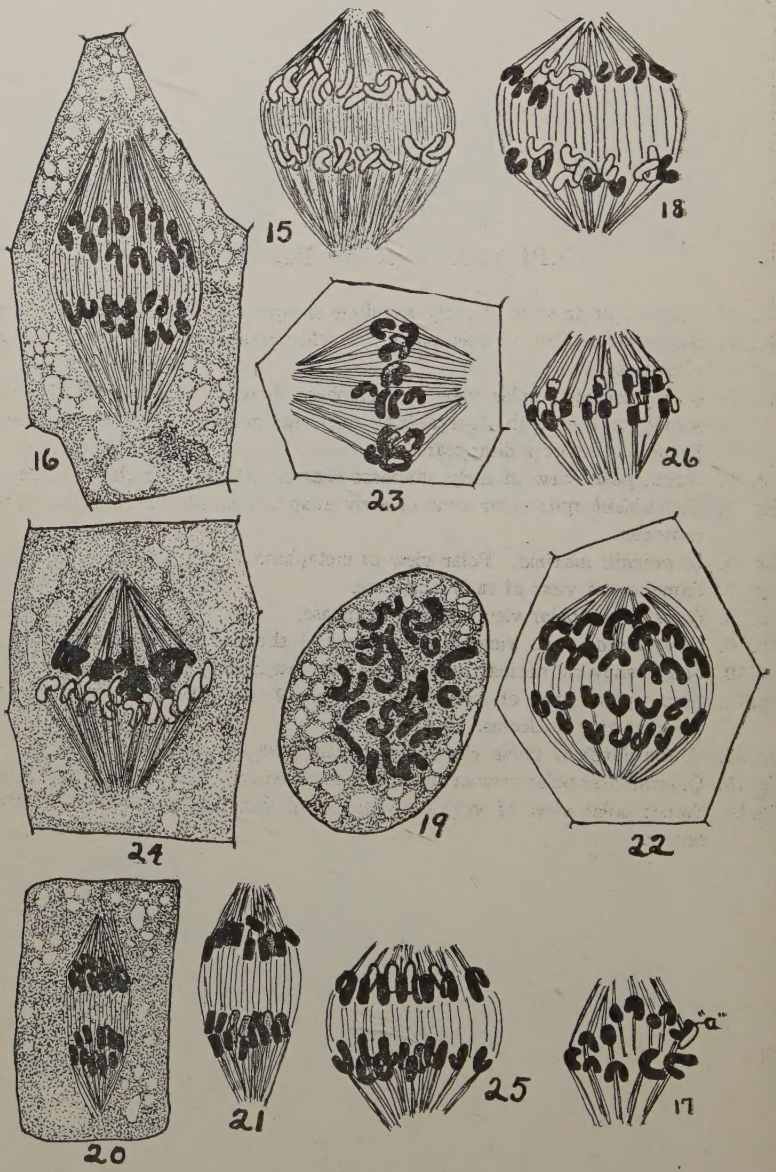
PLATE I



EXPLANATION OF FIGURES

Fig. 1. *Q. alba:* polar view of early anaphase showing 24 daughter chromosomes.
Fig. 2. Same: polar view of metaphase. 13 chromosomes, probably one at "a" already split.
Fig. 3. *Q. macrocarpa:* polar view of metaphase showing 12 undivided chromosomes together with disorganizing nucleolus marked "n." Nuclear membrane had entirely disappeared.
Fig. 4. Same: polar view of early anaphase showing 24 daughter chromosomes.
Fig. 5. *Q. muhlenbergii:* polar view of early anaphase showing 24 daughter chromosomes.
Fig. 6. *Q. borealis maxima.* Polar view of metaphase.
Fig. 7. Same: polar view of early anaphase.
Fig. 8. *Q. velutina:* polar view of early anaphase.
Fig. 9. *Q. coccinea:* polar view of early anaphase showing 25 daughters.
Fig. 10. Same: showing normal number (24) of daughters.
Fig. 11. Same: polar view of metaphase showing 12 undivided chromosomes with disorganizing nucleolus, marked "n."
Fig. 12. *Q. marilandica:* polar view of early anaphase showing 24 daughters.
Fig. 13. *Q. prinoides:* polar view of late anaphase showing 12 daughter chromosomes.
Fig. 14. Same: polar view of very early anaphase showing 24 daughter chromosomes.

PLATE II



EXPLANATION OF FIGURES

Fig. 15, 16. *Q. alba:* side views of anaphase. Each show 12 daughters going to each pole of the dividing cell.

Fig. 17. *Q. prinus:* oblique view of metaphase. Longitudinal split is visible in chromosome marked "a."

Fig. 18. Same: side view of anaphase. Twelve daughter chromosomes are moving toward each pole.

Fig. 19. *Q. Michauxii:* polar view of early anaphase. Twenty-four daughter chromosomes.

Fig. 20. Same: side view of anaphase. Twelve daughter chromosomes moving toward each pole.

Fig. 21. Same: side view of anaphase. Non-disjunction apparently affected two chromosomes, 14 daughters going to one pole and 10 to the other.

Fig. 22. *Q. muhlenbergii:* side view of anaphase. Twelve daughter chromosomes moving toward each pole.

Fig. 23. Same: side view of very early anaphase. Only 16 chromosomes present.

Fig. 24. *Q. borealis maxima:* side view of early anaphase. Twelve daughter chromosomes moving toward each pole. Tardy separation shown in three cases.

Fig. 25. *Q. velutina:* side view of anaphase showing 12 daughter chromosomes moving toward each pole.

Fig. 26. *Q. prinoides:* side view of very early anaphase showing 12 chromosomes each split longitudinally.